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Availability of phosphate for phytoplankton and bacteria and of labile organic carbon for bacteria at different pCO₂ levels in a mesocosm study

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Abstract

Availability of phosphate for phytoplankton and bacteria and of labile organic carbon for bacteria at different $p\text{CO}_2$ levels were studied in a mesocosm experiment (PeECE III). Using nutrient-depleted SW Norwegian fjord waters, three different levels of $p\text{CO}_2$ (350 μatm : $1\times\text{CO}_2$; 750 μatm : $2\times\text{CO}_2$; 1050 μatm : $3\times\text{CO}_2$) were set up, and nitrate and phosphate were added at the start of the experiment in order to induce a phytoplankton bloom. Despite similar responses of total particulate P concentration and phosphate turnover time at the three different $p\text{CO}_2$ levels, the size distribution of particulate P and $^{33}\text{PO}_4$ uptake suggested that phosphate transferred to the $>10\text{ }\mu\text{m}$ fraction was greater in the $3\times\text{CO}_2$ mesocosm during the first 6–10 days when phosphate concentration was high. During the period of phosphate depletion (after Day 12), specific phosphate affinity and specific alkaline phosphatase activity (APA) suggested a P-deficiency (i.e. suboptimal phosphate supply) but not a P-limitation for the phytoplankton and bacterial community at the three different $p\text{CO}_2$ levels. Although specific phosphate affinity and specific APA tended to be higher in $3\times\text{CO}_2$ than in $2\times\text{CO}_2$ and $1\times\text{CO}_2$ mesocosms during the phosphate depletion period, no statistical differences were found. Responses of specific glucose affinity for bacteria were similar at the three different $p\text{CO}_2$ levels. Measured specific glucose affinities were consistently much lower than the theoretical maximum predicted from the diffusion-limited model, suggesting that bacterial growth was not limited by the availability of labile dissolved organic carbon. These results suggest that availability of phosphate and glucose was similar at the three different $p\text{CO}_2$ levels.

1 Introduction

Rising atmospheric CO_2 concentration changes seawater carbonate chemistry by lowering seawater pH, carbonate ion concentration and carbonate saturation state, and increasing dissolved CO_2 concentration (reviewed by Riebesell, 2004). If global CO_2

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emissions continue to rise on current trends (business as usual), the world oceans will suffer an estimated pH drop of about 0.5 units, which is equivalent to a 3 fold increase in the concentration of hydrogen ions, until the year 2100 (Wolf-Gladrow et al., 1999; Caldeira and Wickett, 2003). While the magnitude of ocean acidification can be predicted with a high level of confidence, its impact on marine organisms, their ecosystems, and biogeochemical cycling are largely unknown.

Studies dealing with biological responses to increasing CO₂ partial pressure (pCO₂) and related changes in carbonate chemistry range from a single-species level in laboratory cultures up to a semi-natural community level in outdoor mesocosms. These studies show that increasing pCO₂ enhances photosynthetic carbon fixation (Zondervan et al., 2001; Leonardos and Geider, 2005) and release of dissolved carbohydrates by phytoplankton (Engel et al., 2004), and also modifies phytoplankton species composition and succession (Tortell et al., 2002). These pCO₂ dependent changes in phytoplankton parameters further enhance growth rate, production as well as α - and β -glucosidase activity of heterotrophic bacteria, especially of attached bacteria (Grossart et al., 2006). On the other hand, no significant increase in primary production (Tortell et al., 2002; Sciandra et al., 2003; Delille et al., 2005), total phytoplankton biomass (Tortell et al., 2002), and total bacterial biomass (Rochelle-Newall et al., 2004, Grossart et al., 2006) have been detected at increasing pCO₂ levels.

The elemental composition (e.g. C, N, P) in living organisms is to a certain extent constrained by the necessity to maintain their metabolism (homeostasis) as compared to the rest of the material world (reviewed by Sterner and Elser, 2002). Changes in pCO₂ dependent carbon production by phytoplankton and bacteria (see above) may alter their nutrient demands. On a global scale, these pCO₂ dependent changes will greatly influence carbon and nutrient cycling in the ocean. However, significant differences in consumption ratio of various inorganic nutrients due to increasing pCO₂ levels have been found in one study (Tortell et al., 2002) but not in an other one (Engel et al., 2005). In this context, changes in nutrient availability for phytoplankton and bacteria at different pCO₂ levels seem to be unclear and, thus need to be investigated in greater

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detail.

Nutrient availability (e.g. deficiency, limitation) is not necessarily easy to be examined especially for natural communities of phytoplankton and bacteria. A recent study suggests that the specific affinity for phosphate uptake and the specific alkaline phosphatase activity (APA), which are phosphate uptake rates (inverse of phosphate turnover times) and APA, respectively, normalized to the summed biomass of phytoplankton and bacteria, are useful to examine phosphate availability for the natural phytoplankton and bacteria community in different P starved aquatic systems (Tanaka et al., 2006). Similarly, specific affinity for glucose uptake, which is glucose uptake rates (inverse of glucose turnover times) normalized to bacterial biomass, can be useful to examine the availability of labile organic carbon for bacteria (Tanaka et al., 2007¹).

The objective of the present study is to examine how the availability of phosphate for phytoplankton and bacteria and of labile organic carbon for bacteria changes at different pCO₂ levels during a mesocosm experiment. Particulate P concentrations, turnover times of phosphate and glucose, and APA were measured during the experiment. Combining these results with biomass measurements of phytoplankton and bacteria (Paulino et al., 2007; Schulz et al., 2007²), we have analyzed specific phosphate affinity, specific APA, and specific glucose affinity.

¹Tanaka, T., Thingstad, T. F., Cardelús, C., Jezbera, J., Lekunberri, I., Sala, M. M., Urein, F., and Gasol, J. M.: Production of non-labile DOC in the microbial food web by excessive addition of nitrogen and labile organic carbon to P-starved coastal waters, in preparation, 2007.

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2 Materials and methods

2.1 Experimental setup and sampling

The experimental setup and sampling has been described in detail elsewhere (Riebesell et al., 2007; Schulz et al., 2007²). Briefly, the mesocosm experiment was carried out at the Espeyrend Marine Biological Station (University of Bergen, Norway) from 15 May to 9 June 2005. Nine mesocosms (polyethylene, ca. 25 m³, 9.5 m water depth) were filled with unfiltered, nutrient-poor, post-bloom fjord water, and were covered by gas-tight tents (ETFE foil). Three different CO₂ concentrations, 350 μatm (1×CO₂), 700 μatm (2×CO₂), and 1050 μatm (3×CO₂), were set up in triplicates by CO₂ aeration (see Engel et al., 2005 for details). To induce the development of a phytoplankton bloom, nitrate and phosphate were added before the start of the experiment (Day –1) to obtain initial concentrations of 14 μmol L^{–1} NO₃ and 0.7 μmol L^{–1} PO₄. A tube sampler (5 m long, 10 cm diameter) was used to collect integrated samples (0–5 m). Samples for particulate P, turnover times of glucose and phosphate, and APA were taken from three mesocosms, M2 (1×CO₂), M5 (2×CO₂), and M8 (3×CO₂).

2.2 Particulate P

Particulate P samples were size-fractionated in triplicates on polycarbonate filters (47 mm diameter) with 10, 5, 1, and 0.2 μm pore sizes, respectively. Filters were transferred to polycarbonate test tubes with 5 ml of Milli-Q water and oxidized by acid persulphate at 121°C. Liberated P was spectrophotometrically measured (Koroleff, 1983). As the mean coefficient of variation was 14% for the >10 μm fraction, 10% for the >5 μm fraction, 11% for the >1 μm and >0.2 μm fractions (n=24 for each fraction), only the mean concentrations were shown for simplicity.

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2.3 Uptake of $^{33}\text{PO}_4$ and ^{14}C -glucose

Uptake rate of orthophosphate was measured using ^{33}P -orthophosphate (Thingstad et al., 1993). Carrier-free ^{33}P -orthophosphate (Amersham, 370 MBq ml $^{-1}$) was added to 12 ml samples in 15 ml sterile Nunc test tubes to give a final radioactivity of $\sim 10^5$ counts per minute ml $^{-1}$. Samples for subtraction of background and abiotic adsorption were fixed with 100% TCA before isotope addition. Samples were incubated under subdued (laboratory) illumination at in situ temperature. Incubation time was short enough to assure a linear relationship between the fraction of isotope adsorbed vs. the incubation time but it was long enough to reliably detect isotope uptake above background levels. Incubation was stopped by a cold chase of 100 mmol L $^{-1}$ KH $_2$ PO $_4$ (final conc. 1 mmol L $^{-1}$). Subsamples were filtered in parallel on 25 mm polycarbonate filters with 10, 5, 1, and 0.2 μm pore sizes, which were placed on a Millipore 12 place manifold and supported on Whatman (GF/C) glass fiber filters saturated with 100 mmol L $^{-1}$ KH $_2$ PO $_4$. After filtration, filters were placed in polyethylene scintillation vials with Ultima Gold (Packard), and radio-assayed. After the radioactivities of the filter were corrected for those of the blank filter obtained from fixed samples, $T_{[\text{PO}_4]}$ (h) was calculated as $T_{[\text{PO}_4]} = -t/\ln(1-f)$ where f is the fraction (no dimension) of added isotope collected on the 0.2 μm filter after the incubation time (t :h).

Uptake of glucose was measured in 20 ml samples incubated with D-[U- ^{14}C]-glucose (Amersham, 7.4 MBq ml $^{-1}$) (Hobbie and Crawford, 1969 modified by Havskum et al., 2003). After 1 h of incubation under subdued (laboratory) illumination at in situ temperature, the sample was split into two. Particulate ^{14}C ($>0.2 \mu\text{m}$) uptake was measured on 10 ml samples filtered on 0.2 μm pore size cellulose nitrate filters, and ^{14}C -CO $_2$ was absorbed on 25 mm Whatman (GF/F) glass fiber filters with 250 μl phenethylamine fixed inside the cap of 20 ml polyethylene scintillation vials containing 10 ml. Filters were placed in polyethylene scintillation vials with Ultima Gold (Packard), and radio-assayed. Turnover time of glucose was calculated as the inverse of the fraction of added isotope consumed per hour. The measurement could not be done between

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Days 0–3 due to a technical problem.

2.4 Calculation of specific affinity for phosphate and glucose uptake

Under the assumption that a community of phosphate users (i.e. bacteria and phytoplankton) consists of a set of n groups with biomass B_i (nmol-P L⁻¹: $i=1, \dots, n$), and all of which take up PO₄ proportional to phosphate concentration ($S_{[PO_4]}$: nmol-P L⁻¹) and to each biomass, one has $\alpha_{[PO_4]i} S_{[PO_4]} B_i = f_i V_{[PO_4]}$, where $\alpha_{[PO_4]i}$ is the specific affinity for PO₄ uptake (L nmol-P⁻¹ h⁻¹) by osmotroph group i and f_i is the fraction (no dimension) of total uptake $V_{[PO_4]}$ that goes into osmotroph group i (Thingstad and Rassoulzadegan, 1999). Since the sum of PO₄ uptake equals to $V_{[PO_4]}$ (sum of $f_i=1$) and PO₄ turnover time is the ratio between the phosphate concentration and the P flux through this pool ($T_{[PO_4]}=S_{[PO_4]}/V_{[PO_4]}$), one obtains

$$\sum_{i=1}^n \alpha_{[PO_4]i} B_i = \frac{V_{[PO_4]}}{S_{[PO_4]}} = \frac{1}{T_{[PO_4]}} \quad (1)$$

Then, the total specific uptake rate (h⁻¹) (Eq. 1) can be normalized to total biomass of bacteria and phytoplankton (B), and is defined as specific affinity for PO₄ uptake by the osmotroph community ($\alpha_{[PO_4]}^e$: hereafter, specific PO₄ affinity):

$$\alpha_{[PO_4]}^e = \frac{\sum_{i=1}^n \alpha_{[PO_4]i} B_i}{\sum_{i=1}^n B_i} = \frac{V_{[PO_4]}}{S_{[PO_4]} B} = \frac{1}{T_{[PO_4]} B} \quad (2)$$

Specific affinity for glucose ($\alpha_{[Glu]}^e$: L nmol-P⁻¹ h⁻¹) by bacteria is defined as

$$\alpha_{[Glu]}^e = \frac{1}{T_{[Glu]} B_{BAC}} \quad (3)$$

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where $T_{[\text{Glu}]}$ is the function of glucose concentration ($S_{[\text{Glu}]}$: nmol-glucose L^{-1}) and its flux ($V_{[\text{Glu}]}$: nmol-glucose $\text{L}^{-1} \text{h}^{-1}$) through this pool ($T_{[\text{Glu}]} = S_{[\text{Glu}]} / V_{[\text{Glu}]}$) and B_{BAC} is bacterial biomass (nmol-P L^{-1}). Since all mesocosms were P-depleted rather than labile organic carbon depleted (see Results) and we wanted to unify the unit of specific affinity, specific glucose affinity was expressed in the unit of P.

To calculate P-biomass, data on bacterial abundance and Chla were used (Paulino et al., 2007; Schulz et al., 2007²). Bacterial abundance and Chla were converted to C-biomass under the assumption that bacterial carbon content is 20 fg C cell⁻¹ (Lee and Fuhrman, 1987) and C: Chla (w:w) is 30 (w:w), respectively. Fixed C:P molar ratios of 106 for phytoplankton (Redfield et al., 1963) and 50 for bacteria (Fagerbakke et al., 1996) were used to calculate P biomass of bacteria and phytoplankton, respectively. Although C:P ratios are variable for both phytoplankton and bacteria (e.g. Fagerbakke et al., 1996; Geider and La Roche, 2002), we applied the average C:P ratios for phytoplankton and bacteria. This is because direct measurement of P biomass of osmotrophs was not done in this study (see Results and Discussion for potential biases by these fixed ratios).

2.5 Alkaline phosphatase activity

APA was measured fluorometrically using 3-O-methylfluorescein-phosphate as substrate (Perry, 1972). Samples were mixed with the substrate solution in 0.1 mol L^{-1} Trizma-HCl pH 8.3 (final concentration 0.1 $\mu\text{mol L}^{-1}$). Fluorescence was measured just after the addition of the substrate solution and at two or three subsequent times according to the fluorescence increase. After correcting fluorescence values of samples to those of autoclaved samples, APA (nmol-P $\text{L}^{-1} \text{h}^{-1}$) was calculated by using a linear regression of fluorescence values versus incubation time. The APA measurement was done only for the period with low concentrations of soluble reactive phosphorus (SRP) (Days 10–25: Schulz et al., 2007²). As APA is derepressed when cellular P falls below a certain threshold level (e.g. Fitzgerald and Nelson, 1966; Rhee, 1973; Mykkestad

and Sakshaug, 1983) and biomass of phytoplankton and bacteria were variable with time and between mesocosms, biomass-specific APA (h^{-1}) was calculated by dividing APA by estimated P biomass of osmotrophs (nmol-P L^{-1}). Measurements of APA and phytoplankton biomass were not always synchronized due to logistic constraint. To calculate specific APA, Chla values on Days 19, 21, and 23 (Data from Schulz et al., 2007²) and APA values on Day 24 were linearly interpolated.

2.6 Statistical analysis

Analysis of covariance (ANCOVA) was done using the R software (<http://www.r-project.org/>) with log-transformation of all data. Experimental day was used as the covariate and pCO_2 was used as the nominal predictor. Simple linear regression (Model I) was used to describe the relationship between specific glucose affinity and dissolved organic carbon (DOC: Data from Schulz et al., 2007²). As the temporal variations of these parameters were similar between the three mesocosms (see Results and Discussion), all data except on Day 4 were pooled for the correlation analysis. Statistical significance of linear regression was tested by *F*-test.

3 Results and discussion

In this study, samples were taken only from one mesocosm of each pCO_2 level (M2, M5, and M8) because of logistic constraints. Since no significant differences between samples of each pCO_2 level were found for temporal changes in inorganic and organic nutrients, biomass and production of phytoplankton and bacteria (ANCOVA test,

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$P > 0.05$: Allgaier et al., 2007³; Egge et al., 2007⁴; Paulino et al., 2007; Schulz et al., 2007²), we assume that the three mesocosms selected in this study were representative for each $p\text{CO}_2$ level.

The increase of total particulate P ($>0.2 \mu\text{m}$) between Days 0–10 was accompanied by an increase of particulate P in the $>10 \mu\text{m}$ fraction in all three mesocosms (Fig. 1). While particulate P concentrations in the $0.2\text{--}1 \mu\text{m}$ fraction varied little except on Day 6 in $3\times\text{CO}_2$ during this period, the proportion of the $0.2\text{--}1 \mu\text{m}$ fraction to total particulate P decreased. The particulate P concentration in the $>10 \mu\text{m}$ fraction peaked on Day 10 in all mesocosms, while it was significantly higher in $3\times\text{CO}_2$ ($0.61 \mu\text{mol L}^{-1}$) than in $1\times\text{CO}_2$ ($0.44 \mu\text{mol L}^{-1}$) on Day 10 (t-test, $P < 0.05$). While the highest proportion of the $>10 \mu\text{m}$ fraction in $2\times\text{CO}_2$ and $1\times\text{CO}_2$ was observed on Day 6 (60% and 71%, respectively), the particulate P concentration in the $>10 \mu\text{m}$ fraction on Day 6 was significantly higher in $3\times\text{CO}_2$ ($0.46 \mu\text{mol L}^{-1}$) than in $2\times\text{CO}_2$ ($0.29 \mu\text{mol L}^{-1}$) (t-test, $P < 0.005$). However, the statistical difference of the $>10 \mu\text{m}$ fraction between $3\times\text{CO}_2$ and $1\times\text{CO}_2$ ($0.38 \mu\text{mol L}^{-1}$) was marginal on Day 6 (t-test, $P = 0.053$). After the peak on Day 10, the proportion of the $>10 \mu\text{m}$ fraction decreased to 33–43%, while that of the $1\text{--}10 \mu\text{m}$ fraction increased to 30–45% in all three mesocosms.

Temporal variations in substrate turnover time reflect either those of substrate concentration or those of substrate flux through this pool or both (see Materials and Methods). Phosphate turnover time varied by factor of ca. 1500 with a range of 0.4 to 625 h (Fig. 2). During the first 6 days when SRP concentrations were high (ca. $0.4\text{--}0.8 \mu\text{mol L}^{-1}$; Schulz et al., 2007²), phosphate turnover time was longest (in the order of 100 h). Between Days 6–12, it rapidly decreased to values in the order of 0.1 h.

³Allgaier, M., Riebesell, U., and Grossart, H.-P.: Microbial response to enrichment in $p\text{CO}_2$ and subsequent changes in phytoplankton and nutrient dynamics, Biogeosciences Discuss., in preparation, 2007.

⁴Egge, J. K., Engel, A., Thingstad, T. F., and Riebesell, U.: Primary production during nutrient-induced blooms at elevated CO_2 concentrations, Biogeosciences Discuss., in preparation, 2007.

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From Day 16 onward, turnover time oscillated (0.4–21 h) and tended to be shorter in $3\times\text{CO}_2$ than in $2\times\text{CO}_2$ and $1\times\text{CO}_2$. When phosphate turnover time was shorter, more phosphate was taken up by the smaller fraction and vice versa. During the initial period (Days 0–6) with turnover time >100 h, $^{33}\text{PO}_4$ uptake by the $>10\ \mu\text{m}$ fraction increased up to 70% in $3\times\text{CO}_2$, while it was up to 50% in $2\times\text{CO}_2$ and $1\times\text{CO}_2$. The mean uptake was highest (47–53%) by the $0.2\text{--}1\ \mu\text{m}$ fraction and smallest (8–11%) by the $5\text{--}10\ \mu\text{m}$ fraction during the experiment. APA ranged from 1.3 to $24.6\ \text{nmol-PL}^{-1}$ (Fig. 3). After SRP depletion around Day 10 (Schulz et al., 2007²), APA increased toward Days 13–15, and the fastest and highest increase in APA was observed in $3\times\text{CO}_2$. After this peak, APA decreased in all three mesocosms. Glucose turnover time was long (>100 h) between Days 4–6, and rapidly decreased to ca. 16 h on Day 14 (Fig. 4). Thereafter, it rapidly increased toward Day 18 (74–91 h) and fluctuated between 39 and 73 h onward. No significant differences in any of the parameters presented in Figs. 1–4 were detected between the different pCO_2 treatments during the experimental period (ANCOVA, $P>0.05$).

Particulate organic matter (POM) and phytoplankton biomass increased from the start of the experiment, peaked around Day 10, and decreased onward, while Si, SRP, and nitrate concentrations changed from replete to deplete during the experiment (Schulz et al., 2007²). This nutrient dynamics can be summarized as follows: (1) no obvious nutrient depletions between Days 0–6, (2) only Si depleted between Days 7–9, (3) Si and phosphate depleted between Days 10–12, (4) Si, phosphate, and nitrate depleted from Day 13 onward. Interestingly, this approximately corresponded to the dynamics of phosphate turnover time: (1) the longest turnover time (>100 h) between Days 0–6, (2) decreasing turnover time between Days 7–11, (3) the shortest turnover time (<1 h) between Days 12–16, (4) increasing turnover time between Days 17–20, and (5) the short-term oscillation between Days 21–24 (Fig. 2). Using these five different phases of phosphate turnover time, the succession of dominant phytoplankton groups based on HPLC pigment analysis (Schulz et al., 2007²) were summarized as follows: Diatoms and Prasinophytes in Phase I, Diatoms and Prymnesiophytes in

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Phase II, Prymnesiophytes and Prasinophytes in Phase III, Prasinophytes, Dinoflagellates, and Diatoms in Phase IV, and Dinoflagellates and Cyanobacteria in Phase V. These results suggest that temporal changes in availability of the inorganic nutrients influenced those of phytoplankton biomass and succession during the experiment.

5 Specific phosphate affinity, which was calculated for the period of low SRP concentrations (Days 10–24: Schulz et al., 2007²), ranged from 4.0×10^{-4} to 1.3×10^{-2} L nmol-P⁻¹ h⁻¹ in the three mesocosms (Fig. 5). As the biomass of phytoplankton and bacteria was similar in all three mesocosms (Paulino et al., 2007; Schulz et al., 2007²), temporal variation of specific phosphate affinity mirrored that of phosphate turnover time. After
10 SRP depletion, specific phosphate affinity increased toward Days 12–16. However, it decreased between Days 16–20, while, between Days 20–24, it showed short-term oscillations and tended to be higher in 3×CO₂ than in 2×CO₂ and 1×CO₂. Specific APA ranged from 0.003 to 0.141 h⁻¹ and peaked 4–6 days later (Day 19) than the APA (Figs. 3 and 5). This was because the temporal changes of the summed biomass of
15 phytoplankton and bacteria were greater than those of the APA between Days 13–19 (Paulino et al., 2007; Schulz et al., 2007²). However, no significant differences in specific phosphate affinity and specific APA between M2, M5, and M8 occurred between Days 10–24 or 25 (ANCOVA, P>0.05).

Tanaka et al. (2006) have recently proposed that either specific APA >0.2 h⁻¹ and/or
20 specific phosphate affinity >0.02 L nmol-P⁻¹ h⁻¹ indicates P limitation, i.e. the growth rate of the existing organisms is reduced due to the P availability, in different aquatic systems. They have also proposed that either specific APA in the order of 0.01 h⁻¹ and/or specific phosphate affinity in the order of 0.001 L nmol-P⁻¹ h⁻¹ indicate a situation less strict than limitation, i.e. P deficiency or suboptimal nutrient supply for phy-
25 toplankton and bacteria community. In this context, specific phosphate affinity and specific APA suggested P-deficiency of the phytoplankton and bacteria community in all three mesocosms between Days 11–24, except for 2×CO₂ and 1×CO₂ on Days 20 and 24 (Fig. 5). We acknowledge that the estimate of P biomass, which was used to determine specific phosphate affinity and specific APA, includes elements of uncertainty

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in this study (see Materials and Methods). However, the estimated P biomass never exceeded the chemically measured particulate P ($>0.2\ \mu\text{m}$) (range: 14–60%, $n=36$). The ratios of POC to particulate P were similar for all mesocosms and slightly higher (mean \pm SD: 129 ± 28 , $n=38$) than the Redfield ratio of 106 (see Schulz et al., 2007² for POC data). If the specific phosphate affinity is recalculated by correcting the assumed C: P ratios by the POC to particulate P ratios, only for one occasion ($3\times\text{CO}_2$ on Day 23) we found P-limitation whereas all other data points indicated P-deficiency. Thus, we believe that the uncertainties in P biomass estimation would not significantly change our conclusion of phosphate availability for the phytoplankton and bacteria community. During the P deficient period, viral abundance was high in all three mesocosms (Larsen et al., 2007), suggesting that DOM production increased because of viral lysis of bacterial and phytoplankton cells. However, DOP concentrations increased gradually and slightly throughout the experiment (Schulz et al., 2007²). This can be explained by the fact that DOP produced via viral lysis is rather labile, and thus rapidly degraded by DOP hydrolyzing enzymes such as APA (Berman, 1969) and 5'-nucleotidase (Ammerman and Azam, 1985). Both enzymes are essential for PO_4 uptake by osmotrophs from organic compounds when the phosphorus demand is in excess compared to the available phosphate pool.

Specific glucose affinity between the three mesocosms varied similarly with a range of 5.8×10^{-5} to $5.4\times10^{-4}\ \text{L nmol-P}^{-1}\ \text{h}^{-1}$ (Fig. 6). It increased toward Day 9 and gradually decreased onward. The differences in temporal variation between turnover time and specific affinity were due to the large temporal variations in bacterial biomass (Fig. 4; Paulino et al., 2007). Linear regression analysis showed a significant negative relationship between specific glucose affinity and DOC concentrations ($r^2=0.390$, $P<0.0006$, $n=26$). This suggests that the temporal changes in DOC concentration of this study largely related to those of the labile DOC fraction (Fig. 7). This may be explained by DOC production through DIC overconsumption by phytoplankton (Riebesell et al., 2007). In order to examine substrate availability for osmotrophs, the experimentally determined specific affinity (α^e) can be compared with the theoretical maximum

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(α^{\max}). A theoretical expression for the maximum specific affinity for a spherical cell of radius r can be derived (Thingstad and Lignell, 1997):

$$\alpha^{\max} = \frac{3D}{\sigma r^2} \quad (4)$$

where D is the diffusion constant for the substrate molecules, and σ is the volume specific constant of the element in question. If we assume that bacterial cells have a density of 1.2 g cm^{-3} , 50% dry weight of wet weight, 50% carbon of dry weight, a C:P ratio of 50 (Fagerbakke et al., 1996), and a cell radius of $0.25 \mu\text{m}$ and that the diffusion constant for glucose is $6 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ (e.g. Koch, 1971), the maximum specific affinity given by diffusion limitation of substrate transport is calculated to be $0.207 \text{ L nmol-P}^{-1} \text{ h}^{-1}$. The theoretical maximum is 3–4 orders of magnitude higher than the values calculated in this study (in the order of 10^{-5} to $10^{-4} \text{ L nmol-P}^{-1} \text{ h}^{-1}$, Fig. 6). This suggests that bacterial growth was not limited by the availability of labile DOC.

Riebesell et al. (2007) report that enhanced DIC overconsumption was observed in higher pCO_2 levels toward the peak of phytoplankton bloom (Day 12), but the ratio of POC to PON remained very close to the Redfield ratio at the three pCO_2 levels. While this deviation between DIC/ NO_3 drawdown and POC/PON build-up was attributed to enhanced DOC production in higher pCO_2 levels, higher loss of organic C from the upper mixed layer in higher pCO_2 levels suggests enhanced export of POC including transparent exopolymer particles (TEP) originated from DOC (Riebesell et al., 2007). A difference in cumulative primary production between the three pCO_2 levels became evident after the peak of phytoplankton bloom or during the nutrient depleted period (Egge et al., 2007⁴). Whereas contribution of picophytoplankton to total phytoplankton biomass was relatively small in all mesocosms (Riebesell et al., 2007; Paulino et al., 2007), the difference was mainly due to enhanced organic ^{14}C production in the $0.2\text{--}1 \mu\text{m}$ fraction in higher pCO_2 levels, a fraction overlapping TEP size (Egge et al., 2007⁴). Small and intermediate sized phytoplankton groups increased their importance relative to diatoms toward the end of the experiment (Paulino et al., 2007; Schulz et al.,

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2007²). This size shift of the phytoplankton community should have reduced vertical sinking flux, but the loss of organic C from the upper mixed layer continued toward the end of the experiment and was consistently higher at higher pCO₂ levels (Riebesell et al., 2007). The results thus indicate that nutrient depletion (e.g. P deficient, Fig. 5) reduced the bacterial capacity to degrade organic C despite increased labile DOC at higher pCO₂ levels, and may suggest that DOC or small C-rich organic particles, such as TEP, developed into sinking particles.

In summary, all parameters measured in the current study did not show statistically significant differences between the three mesocosms, and were thus apparently independent of different pCO₂ levels. In the accompanying studies, effects of increased pCO₂ level were, if found, relatively small and appeared toward the end of the experiment (Allgaier et al., 2007³; Egge et al., 2007⁴; Paulino et al., 2007; Schulz et al., 2007²). Although phosphate availability tended to be lower in the 3×CO₂ mesocosm compared to the mesocosms toward the end of the experiment, no statistical differences were detected. This may be partly due to the lack of parallel measurements (one mesocosm for each pCO₂ level). However, such small differences could be explained by variance between “parallel treatments” rather than “different treatments” (Martínez-Martínez et al., 2006). These results suggest that availability of glucose and of phosphate availability was similar between three pCO₂ levels. This implies that the plankton food webs can buffer to a large extent the effects of increased pCO₂ and the related changes in carbon chemistry changes during a short time frame (ca. 1 month).

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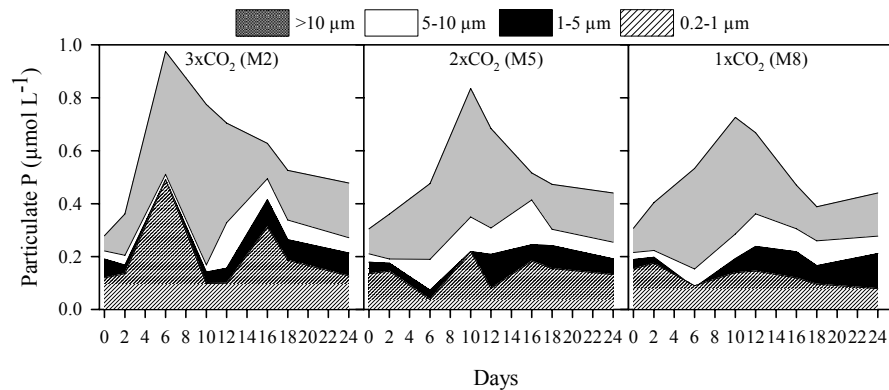


Fig. 1. Responses in concentration ($\mu\text{mol L}^{-1}$) of size-fractionated particulate P.

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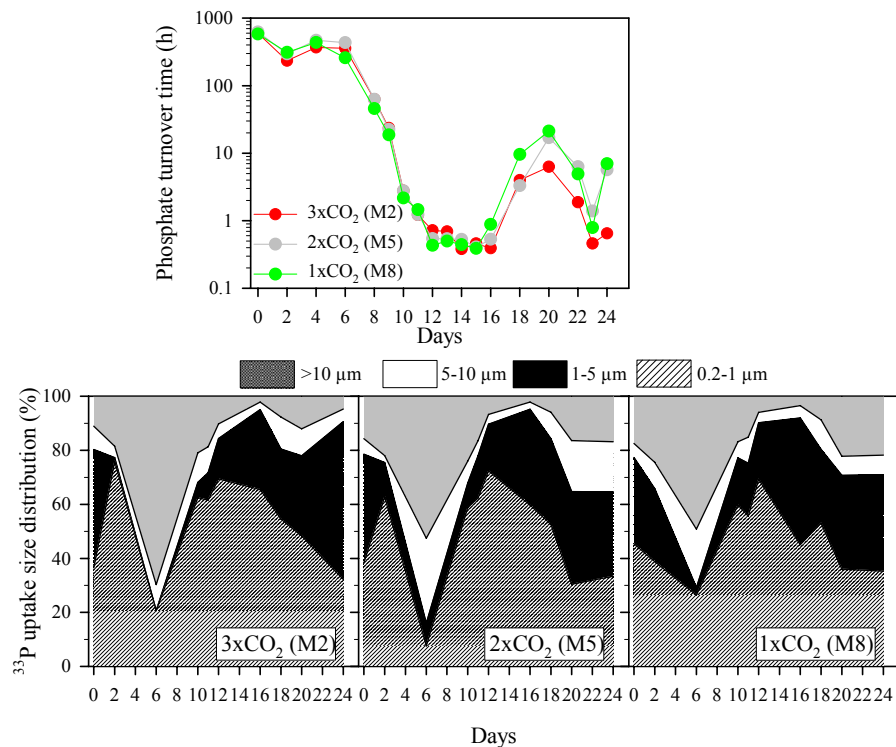


Fig. 2. Responses of phosphate turnover time (h) (top) and size-fraction (%) of ³³PO₄ uptake (bottom).

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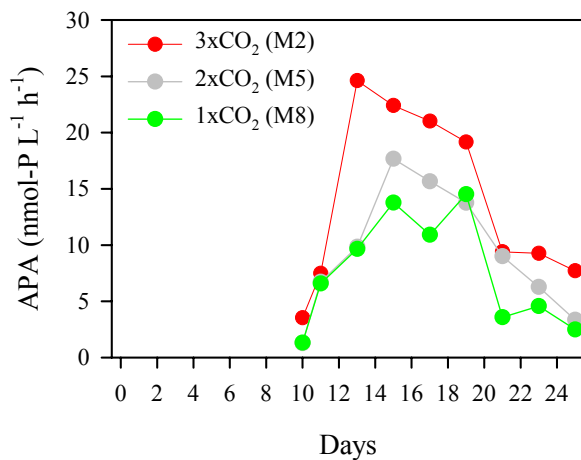


Fig. 3. Responses of alkaline phosphatase activity (APA: $\text{nmol-P L}^{-1} \text{h}^{-1}$).

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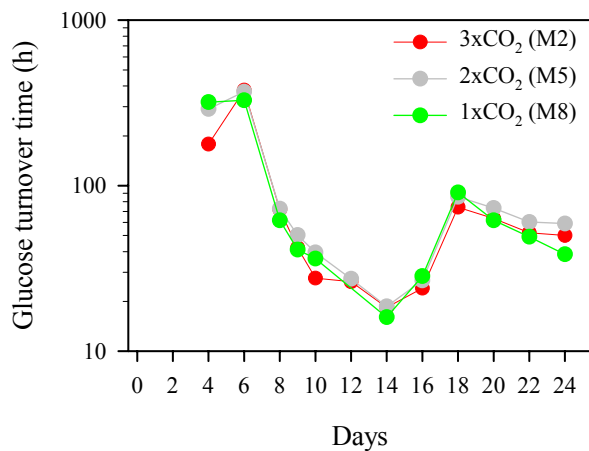
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**Fig. 4.** Responses of glucose turnover time (h).

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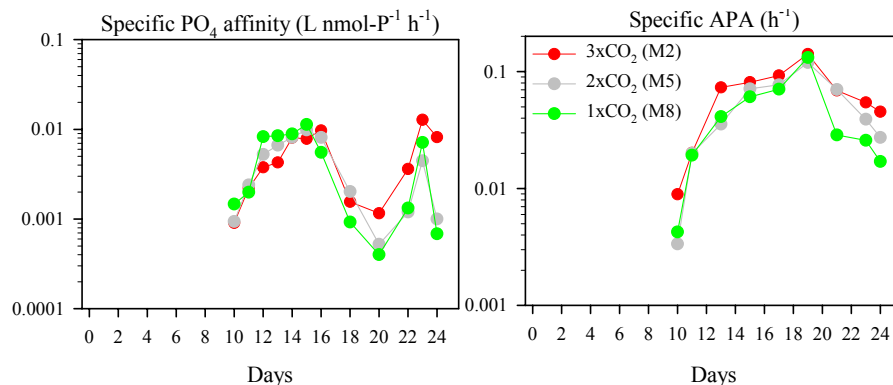


Fig. 5. Responses of specific phosphate affinity ($\text{L nmol-P}^{-1} \text{h}^{-1}$) (left) and specific APA (h^{-1}) (right).

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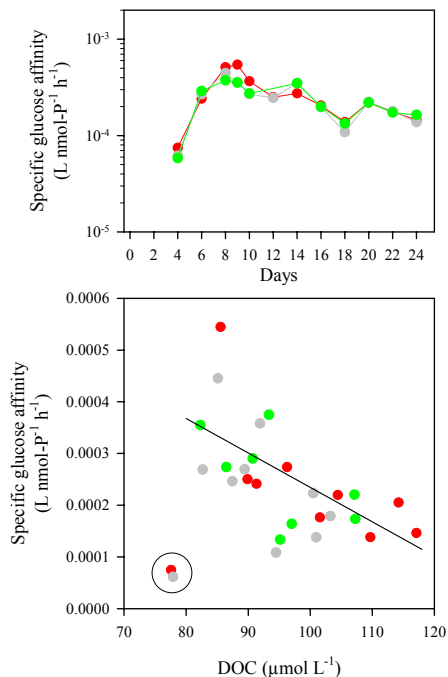


Fig. 6. Responses of specific glucose affinity ($\text{L nmol-P}^{-1} \text{h}^{-1}$) (top), and relationship between specific glucose affinity and dissolved organic carbon (DOC: $\mu\text{mol L}^{-1}$) (bottom). A solid line denotes a Model I linear regression ($[\text{Specific glucose affinity}] = -6.7 \times 10^{-6} [\text{DOC}] + 0.0009$, $n=26$, $r^2=0.390$, $P<0.0006$). Two data in the circle (M2 and M5 on Day 4) are not included for the regression analysis. The DOC data are from Schulz et al. (2007)².

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